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# DYNAMIQUE DES TROUÉES AU LABRADOR

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# SMALL-SCALE GAP DYNAMICS IN CENTRAL LABRADOR

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# RÉSUMÉ

Au fur et à mesure que le cycle de feu se prolonge, les perturbations naturelles mineures, causant des ouvertures ou des trouées dans le couvert forestier, augmentent en importance. Dès lors, elles influencent davantage la dynamique et la structure forestière. Au Labrador, le cycle de feu peut aller au-delà de 400 à 500 ans; un nombre d'années largement supérieur à la longévité des espèces dominantes de la strate arborescente. De cette manière, le développement de la structure forestière et l'établissement de la régénération varient d'un endroit à un autre selon la fréquence des feux et selon les espèces favorisées après le passage d'un feu.

Cependant, à ce processus de régénération post-feu, il ne faut pas négliger les conditions du stand qui influent sur la composition en espèces, la taille des arbres et la susceptibilité aux pathogènes et aux chablis. Des études antérieures ont supporté deux hypothèses de dynamique des espèces dans ce type de forêt : la dynamique des espèces est influencée par les trouées qu'engendrent les perturbations, ou la différence des espèces s'établissant suivant une perturbation est causée par la productivité du stand. Nous émettons donc l'hypothèse que la densité de conifères est influencée par la taille de trouée, la productivité du stand ou de la combinaison de ces deux facteurs.

Dans cette région boréale, l'épinette noire et le sapin baumier sont les deux espèces dominantes. En raison de leurs tolérances à l'ombre et de leurs caractéristiques de croissance différentes, il nous porte à croire que le sapin baumier, espèces à croissance rapide, sera plus abondant que l'épinette noire dans les stands plus productifs. Étant donné que l'épinette noire a un spectre de croissance plus vaste et une tolérance à l'ombre moins élevée que le sapin baumier, nous pensons que l'épinette noire sera plus abondante dans les grandes trouées et ceci, indépendamment de la productivité du stand. De plus, l'absence d'insectes défoliateurs dans les stands pauvres nous laisse envisager un renouvellement continu des individus d'une même espèce en sous couvert, en d'autres mots la régénération suit une tendance de remplacement cyclique.

Afin de déterminer l'importance de la dynamique de trouées dans les forêts du centre du Labrador, nous avons étudié de vieux peuplements d'épinette noire (*Picea mariana* (Mill.) B.S.P.) – sapin baumier (*Abies balsamea* (L.) Mill.) selon un gradient de productivité (faible, moyen et élevé). Un total de dix-huit transects (300 m de long) ont permis d'étudier le régime de trouées

où les données suivantes ont été recueillies pour chacune des trouées interceptant un transect : la taille de la trouée, le dénombrement des arbres créateurs de la trouée ainsi que le nombre d'arbres se retrouvant à l'intérieur de la trouée. La proportion de trouées était relativement élevée avec 47 % pour l'ensemble des trois peuplements. La taille des trouées était petite (une moyenne de 65 $m^2$ – 139 $m^2$), mais elle était significativement différente selon la productivité du stand; les grandes trouées étant plus fréquentes dans le stand le plus productif. La densité de régénération des conifères variait significativement selon la productivité du stand, mais non selon la taille des trouées. Les sapins baumiers étaient plus abondants dans le stand le plus productif, tandis que les épinettes noires étaient plus nombreuses dans les peuplements faiblement et moyennement productifs. Une proportion équivalente entre les arbres créateurs de trouées et la régénération indiquent un remplacement cyclique alors que des recherché préliminaires de dendroécologie supporte que l'établissement de la régénération est régulier, voire un remplacement continu.

Ces résultats démontrent que les caractéristiques des trouées ne sont pas des indicateurs adéquats de la succession forestière à cette latitude. De plus, la productivité forestière est le principal facteur de détermination de l'établissement de la régénération dans ces forêts. Conséquemment, les pratiques sylvicoles visant à émuler les perturbations forestières risquent de ne pas avoir l'effet escompté sur la régénération. Cependant, la formation de trouées entraîne une hétérogénéité de la structure indépendamment de la productivité, ceci étant reconnu comme ayant une influence indirecte sur la faune. Conséquemment, les pratiques traditionnelles d'aménagement forestier équienne (coupe totale) demandent donc à être modifiées afin de répondre plus adéquatement à cette différence.

MOTS-CLÉS : sapin baumier, épinette noire, trouées, productivité, densité de régénération

## ABSTRACT

When fire cycles are long, small-scale disturbances that create openings, or gaps, within a forest landscape likely have increased importance on forest dynamics and forest structure. Fire cycles in Labrador can exceed 400-500 years, which is greater than the longevity of the dominant trees. Hence, structural and regeneration patterns likely differ from areas where fires tend to be more frequent and where most tree replacement occurs following fire induced mortality. However, these patterns can also be significantly affected by stand conditions, which in turn affects species composition, tree size, and their susceptibility to wind and pathogens.

Previous work has supported two alternate hypotheses for species dynamics in these forests: (1) species dynamics are influenced by gaps created by disturbances, or (2) different species recruit preferentially in stands of different productivity. We thus hypothesized that conifer density is influenced by either gap size, stand productivity, or a combination of both.

In this boreal region the dominant species are black spruce and balsam fir. Due to differences in shade tolerance and growth characteristics, we expected faster growing balsam fir to be more abundant than black spruce in high productivity stands. Since black spruce can grow under a wider range of environmental conditions, and is less shade-tolerant than balsam fir, we expected it to be more abundant in larger gaps, regardless of productivity. Further, in the absence of insect defoliators in these species poor stands, we expected to find continuous recruitment from understory individuals of the same species or in other terms – cyclical replacement.

To determine the significance of gap dynamics in forests of central Labrador, we studied mortality and regeneration in old-growth black spruce (*Picea mariana* (Mill.) B.S.P.) – balsam fir (*Abies balsamea* (L.) Mill.) stands that differed in productivity (low, medium and high). A total of 18 linear transects (300m long) were used to sample gap regimes where gap size and gap-maker and gap-filler characteristics were recorded within gaps intersected by each transect. The gap fraction was relatively high (47%) for all three stands. Gaps were small (averaging 65 $m^2$ – 139 $m^2$), but gap size was significantly different among stands of differing productivity, with larger gaps occurring more frequently in high productivity stands. Regenerating conifer density differed significantly between stands of different productivity but not with gap size. Balsam fir was more abundant within high productivity stands while black spruce was more abundant within low and medium productivity stands.

The corresponding gap-maker and gap-filler proportions indicated cyclical replacement, while early dendrochronological analysis indicated regular regeneration establishment for both species (continuous replacement).

These results suggest that gap characteristics are not a useful indicator of forest succession in these high latitude boreal forests. Instead, productivity is the main factor determining species replacement patterns in these forests. Forest management systems that aim to emulate natural gap-phase dynamics may not provide a direct influence on regeneration. However gap formation in all productivity stands creates structural heterogeneity, which although not directly influencing tree species dynamics, has been identified as an important factor for wildlife habitat. Thus traditional even-aged forest management (i.e. clearcutting) may need to be adapted to maintain this forest structure.

KEY WORDS: balsam fir, black spruce, gaps, productivity, regeneration density

# GENERAL INTRODUCTION

## Background

The importance of forest gap dynamics in changing forest structure has been increasingly recognized over the past decade in tropical and temperate forests (Runkle 1981, Runkle 1982, Denslow 1987, Brokaw and Scheiner 1989), and especially in the boreal forest (Kneeshaw and Bergeron 1998, Kneeshaw 2001, McCarthy 2001). This occurs when the death of one or more trees releases growing space to the advantage of advance regeneration or seed propagules (Pickett and White 1985).

In the boreal forest, Kneeshaw and Gauthier (2003) show that old-growth forests are more abundant than previously thought. These old-growth forests have been defined as occurring when the second cohort replaces stems that established after a major disturbance such as fire. Wildfire has been considered the main disturbance in controlling forest dynamics across the boreal forest (Payette et al. 1989, Johnson et al. 1998), however, due to increasing knowledge about fire cycles, this may not be the case (Antos and Parish 2002). In areas where the fire cycle is long, small-scale disturbances, caused by the death of one or more trees that create an opening (or gap) in the canopy, are key processes in forest dynamics (Oliver and Larson 1996, Kneeshaw and Gauthier 2003). In eastern Canada, particularly Labrador, fire cycles often exceed 500 years, a period that is longer than the life span of the tree species present. Thus the landscape is typically dominated by gap-driven, multi-cohort black spruce-balsam fir forests (Foster 1983, Oliver and Larson 1996, Kneeshaw and Gauthier 2003).

## Gap causes

Gaps can be caused by mortality due to low severity fire, insect disturbance, windthrow, fungal attack, or senescence. The cause of mortality influences the degree to which changes in resources and forest structure may occur over time, and so can determine, to some extent, the composition of gap fillers and subsequent forest structure (Dahir and Lorimer 1996, McCarthy 2001).

Insect epidemics, in particular spruce budworm which attacks balsam fir, white, red and black spruce, are known to create conditions which tend to favour the recruitment of balsam fir (the most vulnerable host) from pre-established seedling banks, often resulting in a circular (fir replacing fir), convergent (replacement by fir) or oscillating (fir replaced by w. birch replaced by fir, etc) mode of stand succession (Fye and Thomas 1963, Hatcher 1964, Baskerville 1975, Morin 1994, Bergeron et al. 1995, Kneeshaw and Bergeron 1999). Spruce budworm outbreaks also affect the temporal patterns of seedling recruitment causing the gradual opening of the canopy due to the slow death of budworm-killed trees (MacLean and Baskerville 1979). While several spruce budworm outbreaks have caused defoliation damage in forests neighboring Labrador (e.g. the North Shore region in eastern Québec) (Blais 1983), no such disturbance has been documented in Labrador (Wilton 1965, Roberts et al. 2006, Caron et al. 2009).

Winds can cause trees to uproot or stems to snap (Putz et al. 1983, Oliver and Larson 1996). The direct effect is an increase in growing space by removing shade cast by living trees. Indirect effects in stands include soil

disturbance which creates suitable microstands for the germination of new seedlings (Oliver and Larson 1996, Harrington and Bluhm 2001). Overturned trees mix soil horizons, create hummocky soil conditions (thus creating pit and mound topography), and also expose buried seed banks. The pits and mounds created by windthrow, in addition to the windthrow itself, can provide protection for regenerating plants against desiccating winds and animal browsing (Peterson and Pickett 1995). Peterson and Pickett (1995) also found greater species richness and a higher composition of shade-intolerant species in wind disturbed areas than in the intact forest. They attributed this to increased resource availability following canopy removal, and the creation of a range of microstands that may favour the establishment of a wide variety of species. This freshly disturbed soil experiences higher light and temperature levels, better oxygenation, and different microbial components which can facilitate germination of some pioneer species (Putz 1983). These microstands may be especially important in the boreal forest where the forest floor is often covered by a thick carpet of moss (Bonan and Shugart 1989, Ulanova 2000).

The role of pathogens has rarely been studied as a disturbance factor in boreal forests (McCarthy 2001). Root diseases, such as *Armillaria* and *Inonotus tomentosus*, are the most serious cause of disease loss in Canadian forests affecting approximately 21 conifer species, including black spruce and balsam fir (Mallett 1992, Whitney 2000). As root and butt rot progresses, trees become more susceptible to other factors such as windthrow and other pests (Mallett 1992). The occurrence of some pathogen species can be related to tree age and soil moisture, where frequency increases with age of black spruce but decreases with moisture (Whitney 1995).

The creation of gaps by senescence may be due to the interaction of many factors (Worrall and Harrington 1988). Manion (1981) has for example proposed that tree death is due to both predisposing factors and inciting stresses. Pathogens, partial windthrow and insects may thus also act as inciting stresses causing weakened trees to die. In some forests (i.e. those where other disturbances are minor), gaps due to senescence may represent the principal cause of disturbance (Bartemucci et al. 2002).

## The influence of gaps on forest dynamics

At the community and species scale, single and multiple tree gaps influence the patch structure of forest ecosystems. Gaps can vary in size, and regeneration can occur from buried seeds or rhizomes, advance regeneration, or gaps can be closed from the lateral growth of branches from trees at the edge of the gap. Generally, small openings are closed quickly through the encroachment of existing canopy trees, while larger openings favour the growth of advance regeneration and the establishment of new individuals including pioneer species (Veblen et al. 1989, Dyer and Baird 1997, Clinton and Baker 2000). Pioneer species are more common in large openings as these openings contain greater light levels than small gaps which is crucial since most pioneer species are shade intolerant. Kneeshaw and Bergeron (1999) also show that pioneer species are more likely to be present in the northern part of large gaps. The recruitment of pioneer species can also be favoured in gaps formed by uprooted trees as they result in the creation of exposed mineral soil which acts as a preferred microstand (Putz 1983) for small-seeded species like paper birch.

To evaluate whether gaps have an impact on changing forest structure one can either compare the understory plant community inside a gap with that occurring outside the gap (e.g.: White et al. 1985), or one can compare the understory plant community's characteristics along a gradient of gap characteristics (e.g. Coates 2002). The first approach may be inaccurate in high latitude forests since the impact of a gap in the understory is believed to extend further than the "actual gap" or even the "extended gap" areas (sensu Runkle 1982, Canham et al. 1990, Ban et al. 1998). We used the second approach, comparing the impact along a gradient of gap sizes and forest productivity. An increase of sapling density with gap size has been reported in many studies in the boreal forest (Liu and Hytteborn 1991, Kneeshaw and Bergeron 1998) as well as in other types of forests (Brokaw 1985, Lawton and Putz 1988), however it has not always been observed (Runkle 1982, Lertzman 1992, Abe et al. 1995, Coates 2002, Gagnon et al. 2004). Compositional differences may also be observed as shade-intolerant and shade-tolerant species respond differently to a gradient of gap sizes (Runkle 1982, Brokaw 1985, Brokaw and Schreiner 1989, Kneeshaw and Bergeron 1998). However shade-intolerant species were not important in our stands; the two major tree species occurring in the Labrador study area (black spruce and balsam fir) are both shade tolerant.

Forests with small gap regimes often have comparable gap size distributions; however, tree replacement processes may be different and in time lead to dissimilar outcomes (Dahir and Lorimer 1996). Each type of disturbance may differ by: producing different gap sizes, various degrees and rates of canopy openness, disrupting soil conditions, and influencing gap filler species, composition and development. While the type of disturbance may create distinct disturbance patterns, stand characteristics also influence the

regeneration process by influencing susceptibility to some types of disturbance, leading to different gap sizes, and determining the composition and abundance of the pre-established plant community. Further, since stand conditions influence tree species composition, tree size, and their susceptibility to wind and pathogens (Turner 1989, Whitney 2000), patterns of disturbance and replacement may vary with stand productivity.

## The influence of species and stand

Since it is assumed that biota are adapted to natural disturbance regimes, forest planners have begun attempting to mimic the characteristics of natural disturbances, termed emulation forestry (Bergeron et al. 1999, Coates and Burton 1997, McRae et al. 2001). Unfortunately, there is little information on gap disturbance regimes that can be used for emulation forestry in our study region in Labrador. This is despite an interest in creating more natural patterns in forestry in this region.

In central Labrador, mature forests are composed almost exclusively of two tree species, black spruce (*Picea mariana* (Mill.) B.S.P.) and balsam fir (*Abies balsamea* (L.) Mill.). In neighboring northeastern Quebec, Pham et al. (2004) noted reciprocal replacement in mixed black spruce-balsam fir stands where saplings of each species regenerate in gaps created by individuals of the other species. However they suggested this was disturbance-mediated, due to the actions of species-specific insect defoliators. In species-poor stands of Labrador, with little evidence of insect defoliation, gap dynamics (sensu Runkle 1981) may create structural rather than compositional changes, where mortality of canopy trees will lead to recruitment from understory individuals of the same species – cyclical replacement

(Baskerville 1975, Harper 2003, Kneeshaw and Gauthier 2003). These stands should demonstrate a multi-layered, uneven-aged structure (Oliver and Larson 1996).

A closer look at replacement patterns can also determine whether gap creation varies temporally. Peaks in mortality can be observed in forests following insect outbreaks (Kneeshaw and Bergeron 1998, Bouchard et al. 2006b,) or wind storms (Ulanova 2000). However in areas where episodic events such as insect defoliators are rare, a continuous pattern of small gap formation is evident (Antos and Parish 2002, Caron et al. 2009). Thus, small-scale disturbances and natural senescence that create canopy gaps have likely increased importance in influencing forest structure than in boreal regions where large scale disturbances are frequent.

These patterns of disturbance and replacement may vary with productivity since stand conditions influence tree species composition, tree size, and their susceptibility to wind and pathogens (Turner 1989, Whitney 2000). A theory of dominance related to stand productivity suggests that in productive forests large stature is correlated with a high rate of resource uptake from the environment, while in unproductive forests it is correlated with the ability to tolerate the conditions that make a stand unproductive and sustain slow growth over time (Grime 1977). Black spruce and balsam fir abundance can vary with stand productivity such that in lower productivity stands, black spruce tends to out-compete balsam fir. However in stands of higher productivity balsam fir can out-compete black spruce (Wilton 1965, Viereck and Johnston 1990). These species also have different longevities with black spruce living on average almost twice as long as balsam fir (Burns and Honkala 1990), though both can remain under the canopy for a long-period until resources, such as light and nutrients, increase in availability. In the

absence of species-specific disturbances, when gaps are created by the death of one or more dominant tree species, self-replacement of black spruce should occur in less productive stands, while reciprocal replacement should occur in more productive stands. Since the different tree species have different longevities and tree composition varies with stand productivity, so should gap regimes.

Research on the effects of gap dynamics on forest regeneration has occurred in tropical, temperate and boreal forests (Runkle 1981, Brokaw 1985, McCarthy 2001). However, the results of such studies are rarely transferable between forest types and even between regions of the same forest (Messier et al 2005). Within the boreal forest, gap research has mainly focused on compositional changes between different gap sizes and light levels to the forest floor (Wright et al. 1998, McCarthy 2001). Due to differences in latitude, species, and disturbance regimes throughout much of the boreal forest, the effect of gap processes on forest regeneration remains unclear. Since conditions vary between stands of different productivity, we compared regeneration between three types of forest stands, classified according to height (as an indicator of productivity), in central Labrador. Stand-specific differences, such as gap size distribution and their dynamics, may explain the dynamic behaviour of these stands (Coates and Burton 1997). Further, the response of flora within these gaps may have important implications for silvicultural systems based on gap dynamics.

## Goals and predictions

The main objectives of our study include: (*i*) determining whether species replacement patterns depend on gap size or stand productivity, (*ii*) determining whether species replacement/mortality patterns are continuous (i.e. due to senescence) or sporadic (i.e. driven by temporal mortality events like wind), and whether these patterns change with forest productivity, (*iii*) and determining whether gap creation patterns can be used in forest management.

Both black spruce and balsam fir form an abundant understory in northern boreal forests, and are thus able to self-perpetuate due to their shade-tolerance (McCarthy 2001). Balsam fir tends to associate with moist seedbeds, and is highly shade-tolerant (Frank 1990, Kneeshaw et al. 2006). Conversely, black spruce can persist under a variety of moisture conditions but is less shade-tolerant than balsam fir (Viereck and Johnston 1990). If both species are present in low productivity stands, then black spruce should out-compete balsam fir and show self-replacement. Further, since black spruce is less shade-tolerant than balsam fir it should be expected to respond more to the increase in light from gap creation, therefore the density of black spruce regeneration should increase with gap size while it could be expected that balsam fir will remain in the understory. If both species are present in high productivity stands, a larger presence of balsam fir should be evident as it can out-compete black spruce in better stands. Since conditions in high productive stands favour quick growth and lead to taller trees, these stands will thus be more susceptible to windthrow. We therefore predict gaps will be larger in the high productivity stands.

There are relatively few simultaneous modes of tree mortality in Labrador (i.e. fire or insect outbreaks), therefore we expect that gap makers will be found across a continuous range of age and decay classes (similar to Pham et al. 2004).

# CHAPTER 1

## DOES GAP SIZE OR STAND PRODUCTIVITY INFLUENCE TREE SPECIES RECRUITMENT IN BOREAL FORESTS OF CENTRAL LABRADOR?

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## *1.1 Introduction*

The importance of forest gap dynamics in changing forest structure has been increasingly recognized over the past decade, especially in the boreal forest (McCarthy 2001). This occurs when the death of one or more trees releases the available growing space to the advantage of advance regeneration or seed propagules (Pickett and White 1985). In the absence of large scale disturbances such as fire and insect outbreaks, smaller openings in the forest canopy caused by individual tree senescence play the main role in determining succession in these forests (Kneeshaw and Bergeron 1998, McCarthy and Weetman 2006). In eastern Canada, including Labrador, the fire cycle often exceeds 500 years, a period that is longer than the life span of the tree species present. Thus the landscape is typically dominated by gap-driven, multi-cohort black spruce-balsam fir forests (Foster 1983, Oliver and Larson 1996, Kneeshaw and Gauthier 2003).

Many studies on gap dynamics have focused on the relationship between regeneration success and gap size. In both tropical and boreal forests greater regeneration density has been found in larger gaps (Kneeshaw and Bergeron 1998, Brokaw 1985, de Römer et al. 2008). More specifically, shade-intolerant species were relatively more abundant in large gaps (Runkle 1984), and shade-tolerant species were more abundant in smaller gaps (Kneeshaw and Bergeron 1998). In the northern boreal forest, where species are mainly shade-tolerant, and the distance between trees can be large (McCarthy 2001), a relationship between gap size and regeneration is not always observed (Pham et al. 2004, St. Denis *In Press*).

Generally, shade-tolerant species exist as advance regeneration and can thus respond well to small gap openings. The two main species present in

our study area are black spruce (*Picea mariana*) and balsam fir (*Abies balsamea*). Black spruce is less shade-tolerant and longer lived than balsam fir, and both species form abundant advance regeneration under closed canopies and can self-perpetuate in forests driven by small gap dynamics (Viereck and Johnston 1990). While a better availability of resources in larger gaps should increase the total density of both species, minor differences in shade tolerance may have a significant effect on the proportion and density of each species in the regeneration layer. Since black spruce is less shade-tolerant than balsam fir, we therefore predicted its density to be higher in larger gaps.

When both species are present in the understory, we expected stand productivity to play a more important role in determining regeneration density. Since seedling growth can vary with stand quality, species, and among individual trees (Oliver and Larson 1996), differences in regeneration growth/patterns among gaps from forest stands of varying productivity should be evident. The growth of balsam fir is more variable than black spruce, as it grows quickly in good stands but barely perceptible in poor stands (Wilton 1965, Viereck and Johnston 1990). Black spruce, on the other hand tends to grow slowly in all stands. Both species can remain under the canopy over a long-period until resources, such as light and nutrients, become more available. Thus, in stands of lower productivity black spruce tends to out-compete balsam fir while the opposite is true in stands of high productivity (Frank 1990). We therefore predicted that the seedling density of balsam fir would be greatest in high productivity stands.

Our specific objectives were to determine whether gap size, stand productivity, or a combination of the two, influenced conifer regeneration in

these old-growth stands. We hypothesized that gap size will be more important than productivity in determining regeneration density, but that the relative proportion of fir will increase as stand productivity increases.

## *1.2 Methods*

### ***1.2.1 Study Area***

The study area is within 50 km of Goose Bay, NL (53° 20' N, 60° 25'W, Figure 1.1) and is part of the Perhumid High Boreal ecoclimatic region (Canada Committee on Ecological Land Classification 1989). This region is characterized by intermittent bogs dominated by *Sphagnum* mosses among well-developed forest stands with a common ground cover of feather moss (*Pleurozium schreberi* and *Ptillium crista-castrensis*). *Picea mariana* and *Abies balsamea* are the most prevalent species and are commonly found on shallow upland soils (Lopoukhine et al. 1975). Other, less common, trees include white spruce (*Picea glauca*), white birch (*Betula papyrifera*), and trembling aspen (*Populus tremuloides*) (Lopoukhine et al. 1975, Canada Committee on Ecological Land Classification 1989).

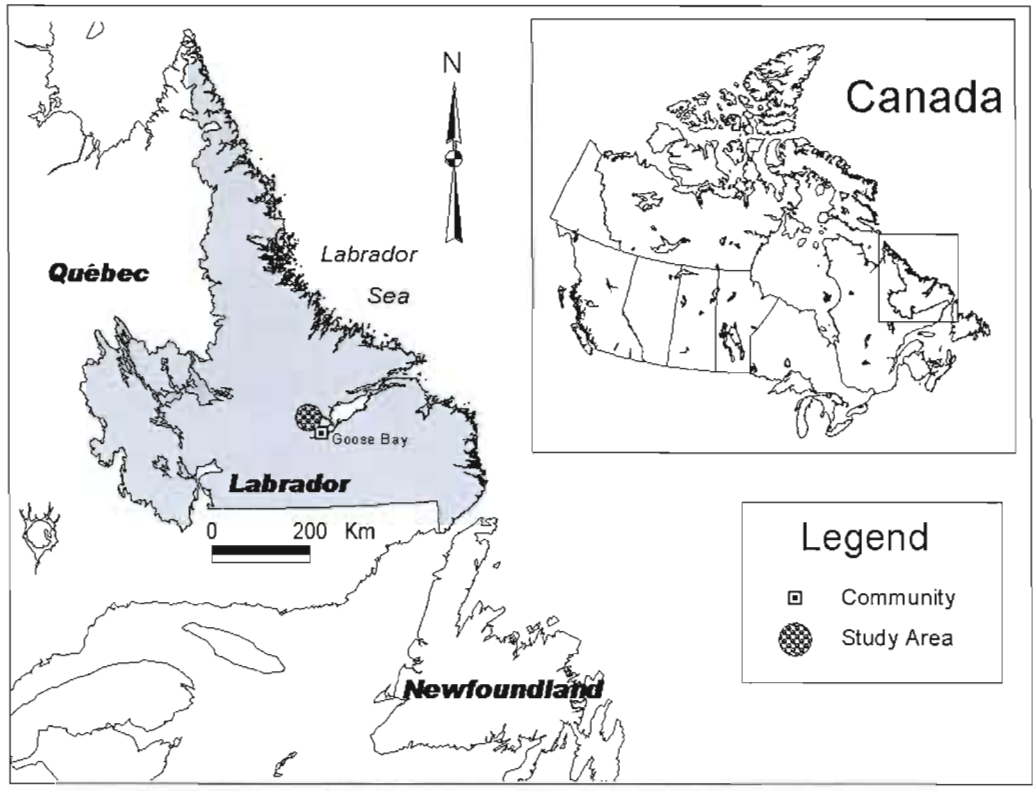



**Figure 1.1 –** Map of study area

### *1.2.2 Data Collection*

Sampling was concentrated in three types of old-growth black spruce-balsam fir stands (> 120 years old as determined by inventory data and validated in the field) of 51 – 75 % crown closure. Stands were identified as low, medium, and high productivity using Newfoundland and Labrador Department of Natural Resources forest cover maps (1:12 500). In these stands, dominant tree heights for low, medium, and high productivity ranged from 9.6-12.5 m, 12.6-15.5 m, and 15.6-18.5 m respectively. These stands represent a productivity gradient as height is a surrogate measure of stand index for

these old-growth forests (Bouchard et al. 2006a, Simon 2005). Previous studies have used vegetation data from similar forest types in Labrador to stratify and validate forest stand types (Simon 2005).

A total of 18 transects (6 per stand type) were sampled, each 300 m in length and 25 m from any forest edge. Gaps intersected by transects were measured using line-intersect sampling, as well as the length (largest distance within the gap) and width (largest distance perpendicular to the length) to determine size using the formula for an ellipse ($A = \pi LW/4$) (Runkle 1981, 1982). In large or irregular shaped gaps, extra width measurements were taken at right angles along the central axis to more accurately determine gap size and form (Kneeshaw and Bergeron 1998). Two measurements were taken for each axis representing the canopy gap (land surface directly under the canopy opening to the edge of the tree crown projection on the ground) and the extended gap (canopy gap plus the area extended to the bases of the canopy trees) (Runkle 1982). Any gaps that were caused by edaphic factors (e.g. rocks, water, etc.) or did not have a defined perimeter were excluded from sampling.

Regenerating trees (gap fillers) were sampled along a variable width belt transect (0.25 – 2 m wide) situated along the longest axis within each gap. The transect size was inversely proportional to the number of seedlings present, to obtain a minimum of 30 – 60 seedlings per gap. The species, height, and dbh (diameter at breast height, for trees > 1.3 m in height) were recorded. Any trees ≥ two thirds of the height of surrounding dominant trees were considered canopy trees rather than regeneration (sensu Pham et al. 2004).

Dead trees (gap makers) were sampled within each gap, and we recorded species, length/height, decay class (see Appendix A figure A1), and mode of mortality (snag, died standing, wind, rot, knocked over, or unknown). To determine the volume of CWD (coarse woody debris) between stand types, we sampled within a subsample of gaps (n = 7 per stand type) and recorded the length, end diameters and dbh (where possible). Volume was calculated using the Smalian Formula (Avery and Burkhart 1994):

$$V = \frac{\frac{\pi T^2}{1000} + \frac{\pi B^2}{1000}}{2} L$$

where:

V = volume of the log in cubic meters,

$\pi$ = 3.141 592 (to 7 significant figures or 6 decimal places),

T = radius of the small end in centimeters,

B = radius of the large end in centimeters,

L = length of the log in meters.

### *1.2.3 Data Analysis*

The percentage of gaps in these stands was calculated as the proportion of the total distance of each transect in canopy opening divided by the total length of the transect (300 m).

Gaps were categorized in 25 $m^2$ increments (i.e. 25 = 0 – 25 $m^2$) and compared using histograms for low, medium, and high productivity. After testing for normality and performing a log transformation, a one-way ANOVA was performed with Minitab 15 (Minitab Inc. 2006) using productivity as the predictor of both expanded and canopy gap size.

Scatter plots were used to compare black spruce and balsam fir regeneration density (stems per $m^2$) among productivity and gap size. Regeneration heights for these species were also categorized (0 – 0.5, 0.5 – 1, 1 – 1.5, 1.5 – 2, and >2 m) and presented using histograms by productivity and gap size. Statistical tests were performed to evaluate the effect of productivity and gap size on both the density and height of regenerating black spruce and balsam fir. Evaluation of the data indicated heteroscedasticity which was then corrected using log transformation. Using ANOVA, we tested the effect of productivity on black spruce and balsam fir density. The densities of both species (combined and separated) were then tested against gap size using linear regression analysis. The average heights of regenerating black spruce and balsam fir were also tested against gap size using linear regression, for each productivity type and with all productivity types combined.

Histograms were used to compare the average volume of gap makers (CWD), their cause of death, and decay class among stand productivity. Using ANOVA, we also tested the effect of productivity on both the volume and decay class of CWD.

## *1.3 Results*

### *1.3.1 Gap Characteristics*

In all three productivity types, extended gaps covered an average of 47% of the 300 $m^2$ transects whereas canopy gaps covered 5-10% less (Table 1.1). Average canopy gap size was 65 $m^2$ and 60 $m^2$ in the low and medium productivity stands respectively and more than doubled to 139 $m^2$ in the high

productivity stands. The analysis of variance found both extended ($P = 0.00$, $F = 11.12$, $R^2 = 0.074$) and canopy gap size ($P = 0.00$, $F = 8.99$, $R^2 = 0.061$) differed significantly by stand type with larger gaps (>100 $m^2$) occurring more frequently in high productivity stands. Smaller gaps (≤100 $m^2$) were more frequent in low (80%) and medium (85%) productivity stands than in high (55%) productivity stands (figure 1.2). Though the gap size distributions for low and medium productivity stands indicated a larger percentage of small gaps, this distribution was not strongly skewed. In contrast, the gap size distribution for high productivity stands resembles a normal distribution, indicating a relatively even distribution of gap sizes. Additionally, few gaps in any stand type were larger than 400 $m^2$ and this was only evident in high productivity stands, where some gaps in particular were too large and interconnected to determine their boundaries.

**Table 1.1** – Canopy and extended gap size characteristics for low, medium, and high productivity stands.

| | | Canopy Gap | | | | Extended Gap | | | |
|---|---|---|---|---|---|---|---|---|---|
| **Productivity** | **N** | **Min** | **Max** | **Mean** | **%*** | **Min** | **Max** | **Mean** | **%*** |
| **Low** | 101 | 5 | 303 | 65 | 38 | 10 | 376 | 91 | 47 |
| **Medium** | 93 | 5 | 313 | 60 | 37 | 12 | 383 | 82 | 47 |
| **High** | 88 | 7 | 457 | 139 | 44 | 12 | 659 | 188 | 49 |

*This indicates the percent of transects covering canopy/extended gaps.

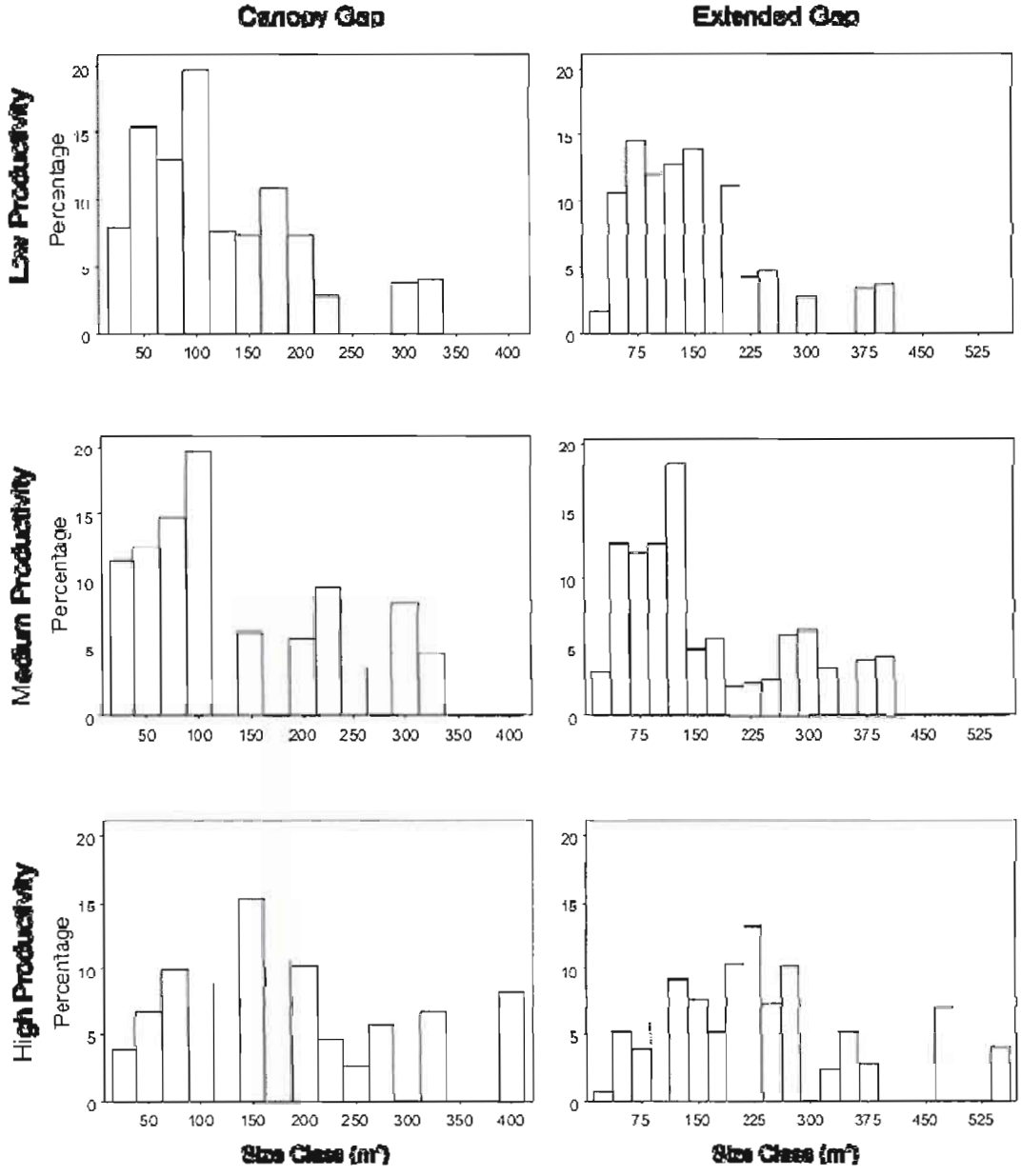



**Figure 1.2** – Percentage of canopy and extended gaps per gap size class ($m^2$) for low, medium, and high productivity stands.

### *1.3.2 Gap Makers*

Even though quite small in size, gaps within low, medium and high productivity stands were created by an average of 10-12 mature trees. Gaps in all three productivity types were formed by a maximum of 25-27 gap makers, with the exception of one extremely large gap in a high productivity stand had a total of 43 gap makers. This gap was an interconnection of many openings, which was an uncommon occurrence in these stands. Approximately 80% of sampled gap makers were identifiable; of which black spruce was the dominant gap maker for low (70%) and medium (74%) productivity stands. The dominant gap maker was balsam fir (55%) for high productivity stands.

There was a significant difference in gap maker volume among stand productivity ($P = 0.009$, $F = 6.12$, $R^2 = 0.41$). High productivity stands had four times the total volume of gap makers than low and medium productivity stands (57.25, 46.46, and 202.93 $m^3$ respectively), and this pattern was similar when evaluated per $m^2$ (Figure 1.3). This is likely due to larger canopy tree heights within these stands.

Most gap makers for low and high productivity stands were present in snag form. However for medium productivity stands, there were equal distributions of gap makers that have either been uprooted due to wind, present in snag form, or decay was too advanced to determine cause of death (unknown) (Figure 1.4). There was no significant difference in the decay class distribution among stand productivity ($P = 0.298$, $F = 1.42$, $R^2 = 0.36$). There was a relatively normal distribution of decay for all three

productivity types, with 70% of gap makers in the earlier stages of decay (decay classes 1 to 3) for low and high productivity stands (Figure 1.5).

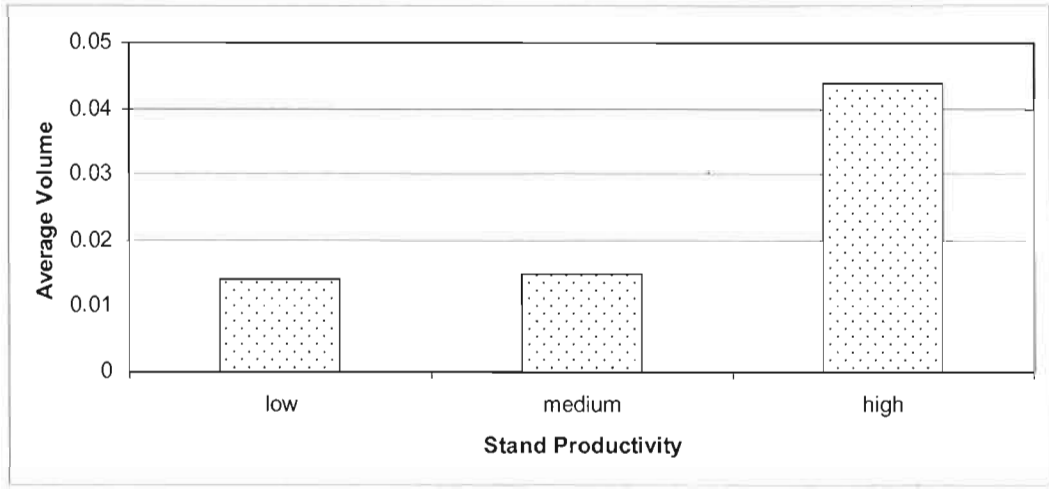



**Figure 1.3** – Average CWD (gap maker) volume per $m^2$ for low, medium, and high productivity stands.

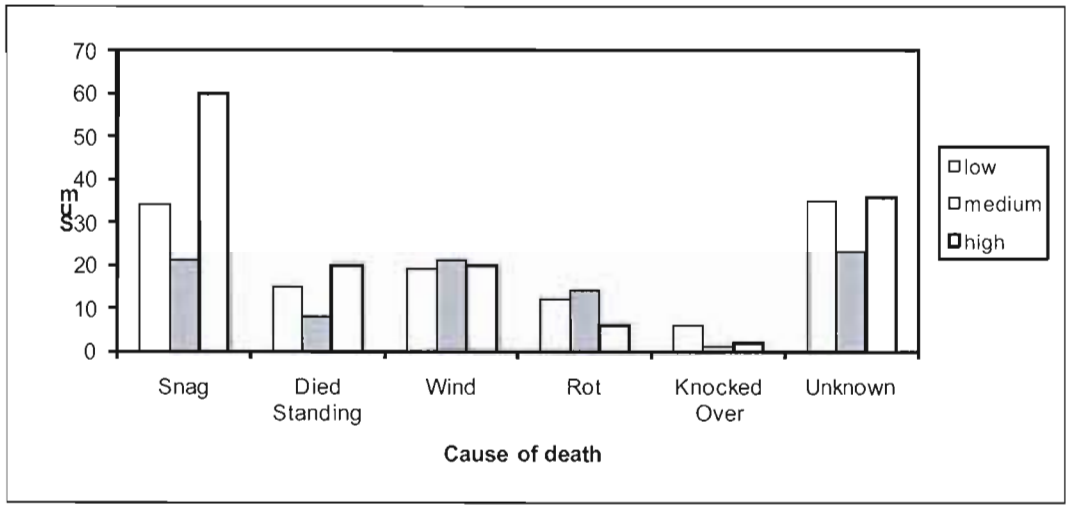



**Figure 1.4** – Distribution of the cause of death per productivity type.

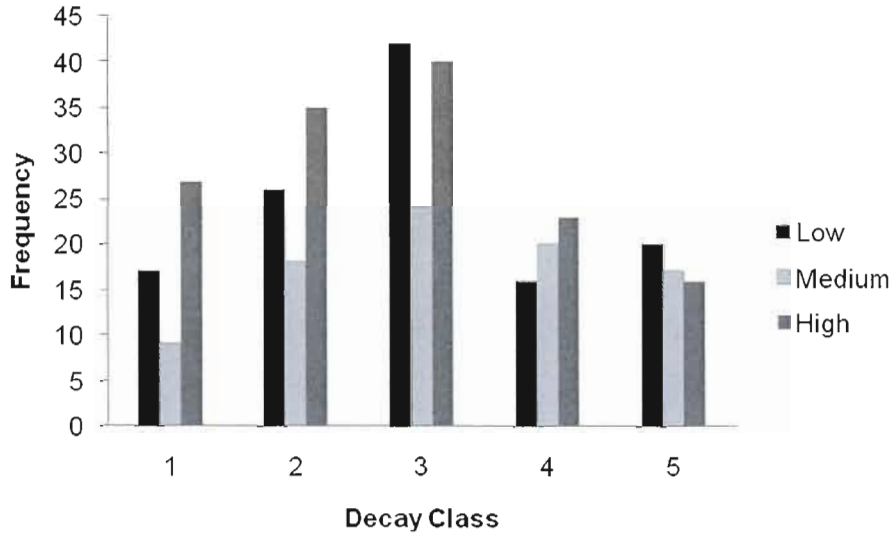



**Figure 1.5** – Frequency of decay class per stand productivity
(For detailed explanation of decay class see Appendix A Figure A1).

### *1.3.3 Gap fillers*

#### *Regeneration Density vs. Stand Productivity*

While there was no difference in total conifer density between productivity types ($P = 0.46$, $F = 0.80$, $R^2 = 0.006$), the density of both regenerating black spruce ($P = 0.00$, $F = 41.18$, $R^2 = 0.23$) and balsam fir ($P = 0.00$, $F = 58.74$, $R^2 = 0.30$) differed significantly between high productivity stands and those that were low or medium productivity. A comparison of gap filler species between productivity types mirrors the pattern of gap makers. There is a sudden shift in species composition between productivity types, where balsam fir is the dominant species in high productivity stands and black spruce is dominant in low and medium productivity stands. However, balsam fir does not have a strong presence in low and medium productivity stands where black spruce density is three times greater than balsam fir. An

average of 3.4, 3.6, and 1.2 stems per $m^2$ were recorded for black spruce while an average of 0.8, 0.5, and 2.9 stems per $m^2$ were recorded for balsam fir for low, medium, and high productivity stands respectively (Figure 1.6). Though balsam fir is dominant in high productivity stands, black spruce has a strong presence, with almost half the density of balsam fir.

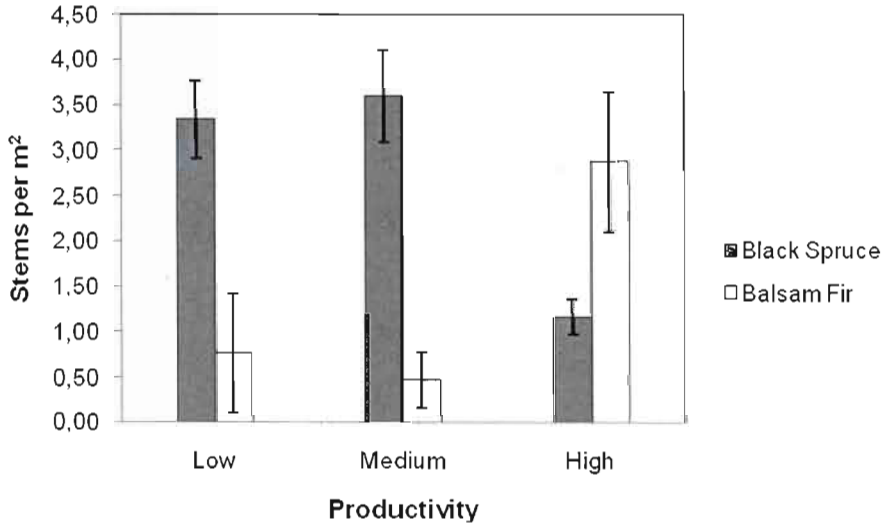



**Figure 1.6** – Average gap-filler density per productivity type.

### *Regeneration Density vs. Gap Size*

After testing the log-transformed data, there was no significant relationship between regeneration density and canopy gap size for all stands combined (Figure 1.7). However balsam fir did show a weak but significant negative relationship with gap size in low productivity stands ($P = 0.00$, $F = 13.05$, $R^2 = 0.118$).

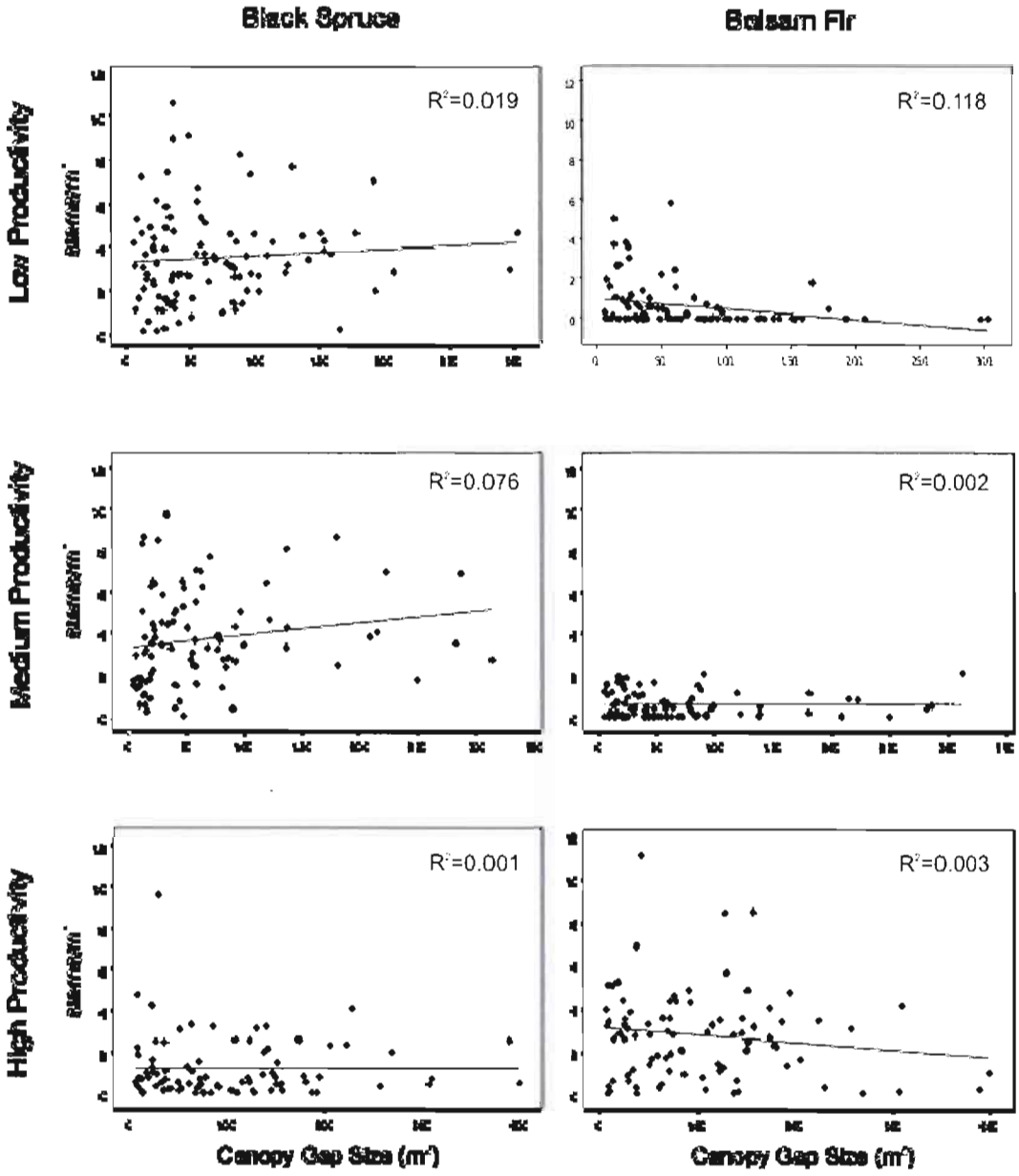
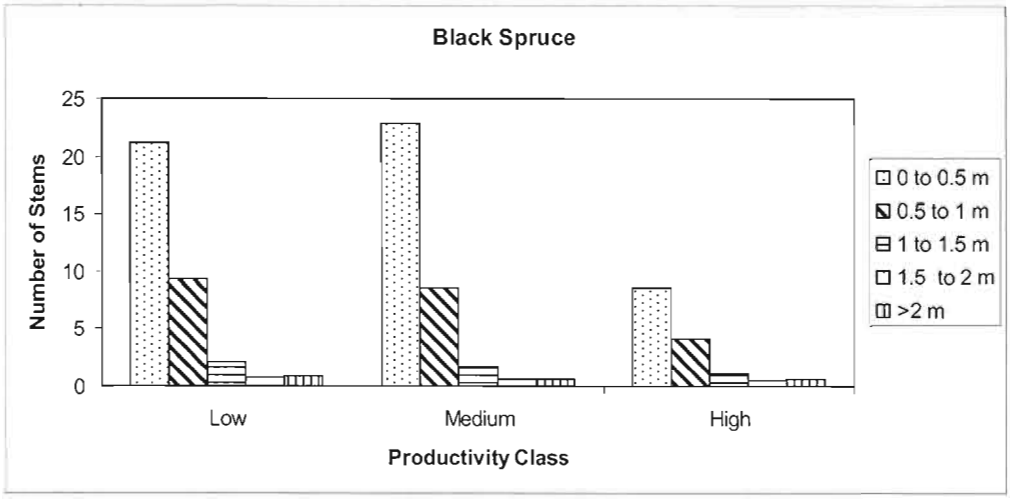



**Figure 1.7** – Relationships between regeneration density and canopy gap size for low, medium and high productivity stands.

### *Regeneration Height vs. Stand Productivity*

More than 85% of regenerating black spruce and balsam fir were ≤ 1 m in height (figure 1.8). When comparing black spruce seedlings less than 1m in height, high productivity stands had fewer stems than low and medium productivity stands. However, this pattern was not similar for black spruce seedlings greater than 1m in height as these larger stems had similar densities in all stands. In contrast, there was an increase in balsam fir seedlings in all size classes for high productivity stands.

a)




b)

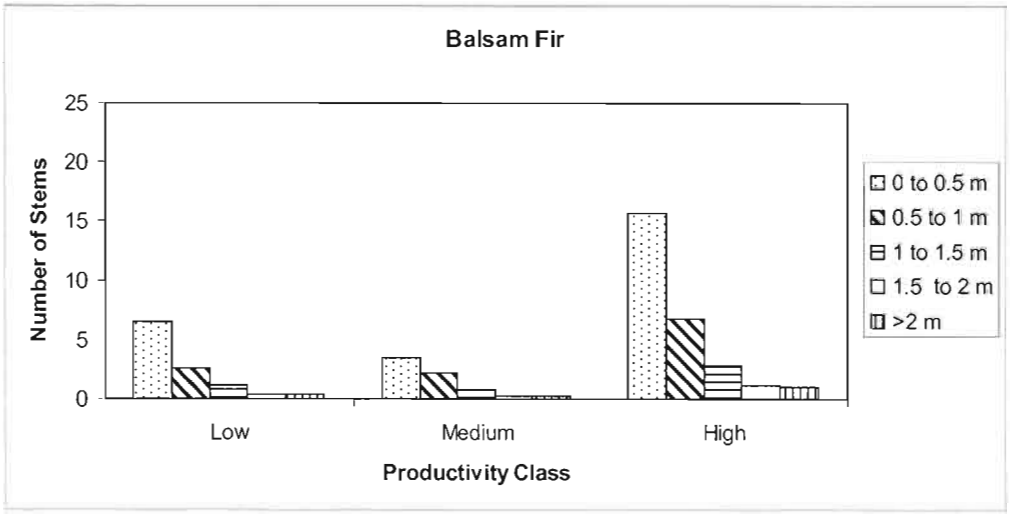
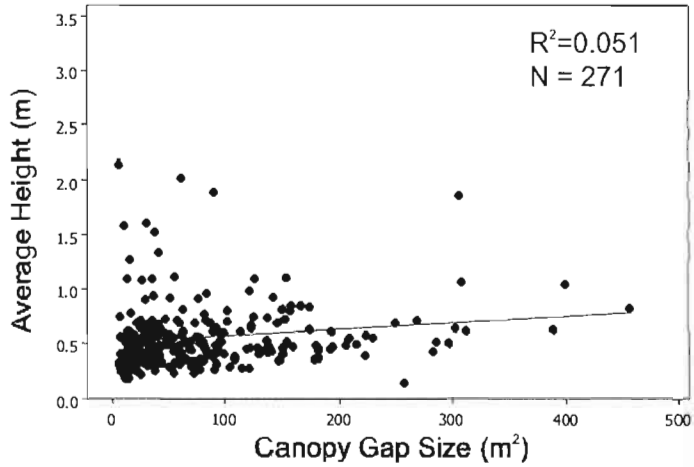



**Figure 1.8** – Average number of (a) black spruce and (b) balsam fir seedlings per gap in each height class for low, medium, and high productivity stands.

### *Regeneration Height vs. Gap Size*

The height of regenerating black spruce increased slightly but significantly with canopy (and extended) gap size ($P = 0.00$, $F = 14.54$, $R^2 = 0.05$) (Figure 1.9a). Results were similar when separated by productivity type: low productivity ($P = 0.019$, $F = 5.66$, $R^2 = 0.06$), medium productivity ($P = 0.018$, $F = 5.79$, $R^2 = 0.06$) and high productivity ($P = 0.025$, $F = 5.26$, $R^2 = 0.07$) (Figure 1.10). There was a lack of a relationship between balsam fir and gap size when stems within each productivity type were tested separately. However, when balsam fir stems for each productivity type were grouped, there was a weak positive relationship with gap size ($P = 0.026$, $F = 5.06$, $R^2 = 0.03$) (Figure 1.9b). This may be due to a small sample size (due to the lack of regenerating balsam fir stems within every gap) in low and medium productivity stands.

a)




b)

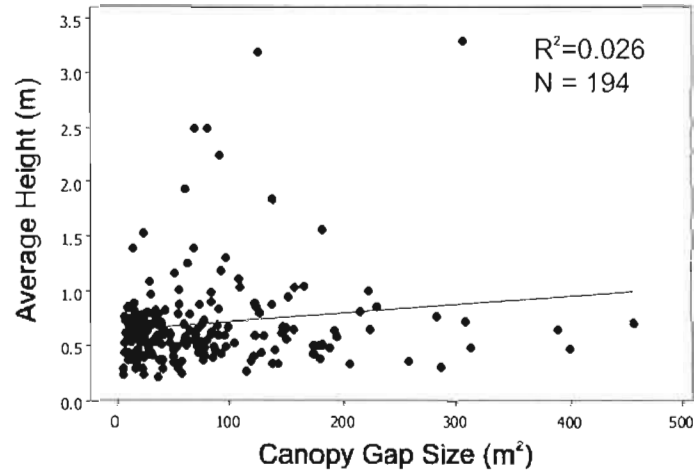



**Figure 1.9** – Relationships between average regeneration height of (a) black spruce and (b) balsam fir and canopy gap size, for all stands combined.

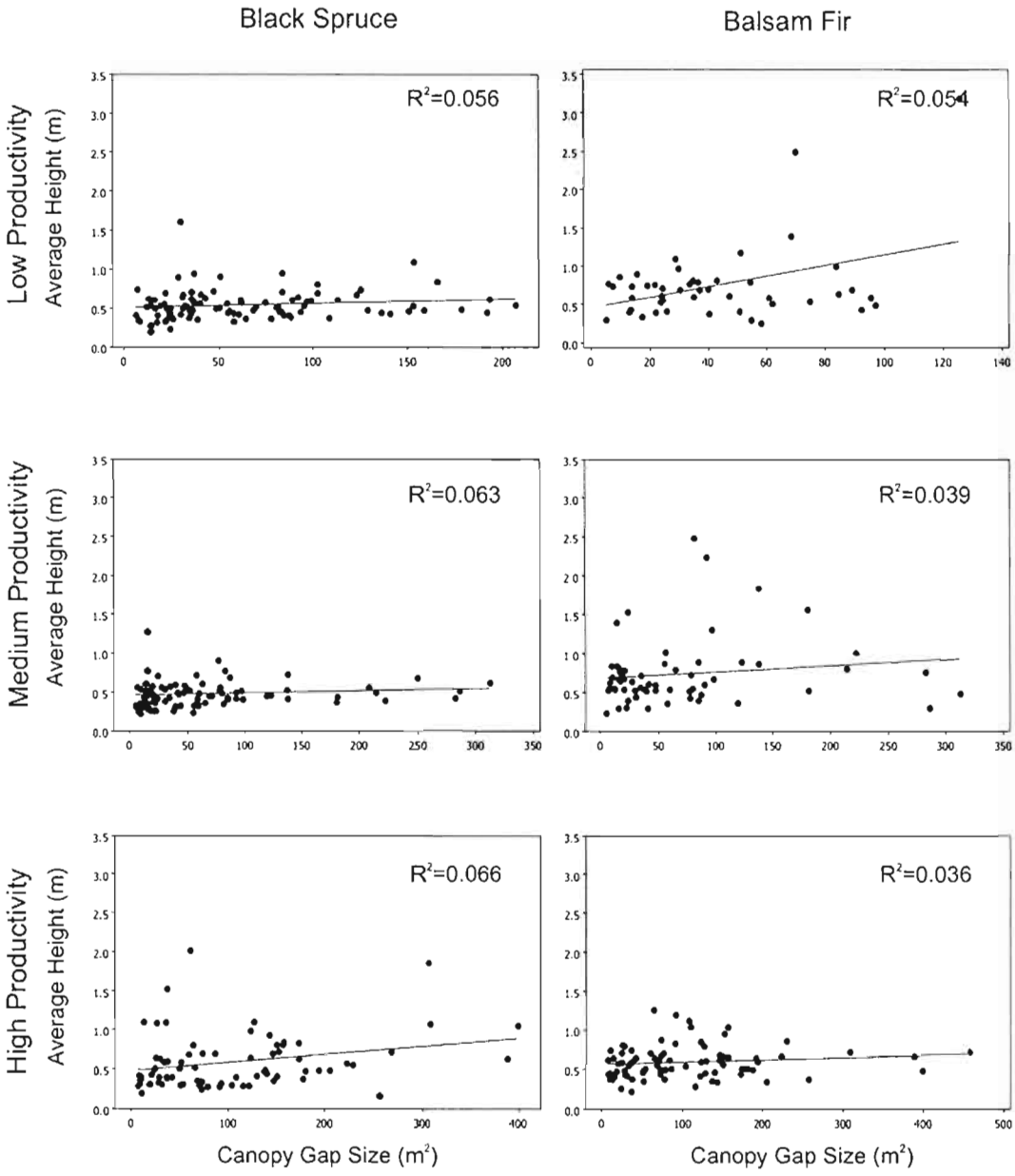
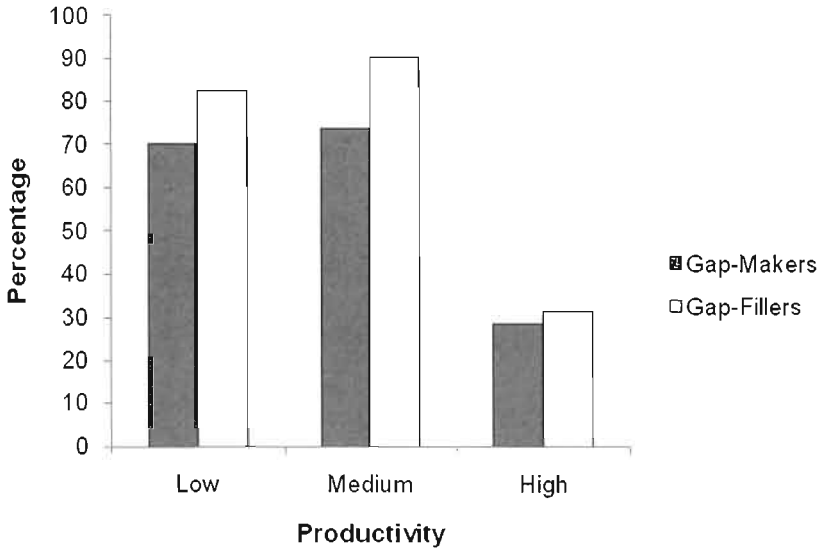



**Figure 1.10** – Relationships between average regeneration height and canopy gap size for low, medium and high productivity stands.

### *1.3.4 Gap Filler – Gap Maker Comparison*

A comparison of the average percent of gap-makers and gap-fillers between different productivity stands illustrate similar proportions (figure 1.11a & b). Black spruce dominates as both gap-maker and gap-filler on low and medium productivity stands (more than 70%) but also has an elevated gap-filler density (31%) within high productivity stands (Figure 1.11).

a) Black spruce




b) Balsam fir

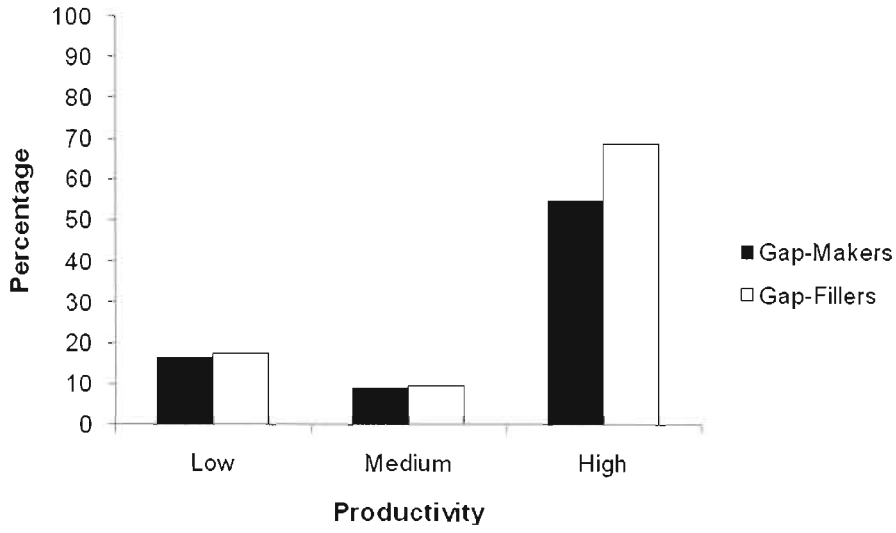



**Figure 1.11 –** Comparison of average percent of (a) black spruce and (b) balsam fir between gap-makers and gap-fillers.

## *1.4 Discussion*

### 1.4.1 Gap regime

The percentage of stand area in canopy gap phase (47%) was comparable to that found by St. Denis (2008), and Harper et al. (2006) but larger than the gap fractions found by others (6% - 36.6%) within the boreal forest (Kneeshaw and Bergeron 1998, McCarthy 2001, Messier et al. 2005) and temperate forest (Runkle 1982). This can be attributed to some common characteristics of coniferous forests at these higher latitudes. In particular, these forests have predominantly open canopies due to narrow conifer crowns, as well as to slow regeneration within each gap due to the short growing season (Bartemucci et al. 2002, Pham et al. 2004).

The distribution of gap sizes differs considerably from those found elsewhere in the boreal forest (Kneeshaw and Bergeron 1998, de Römer et al. 2007). The highest proportion of gaps was not within the lowest size class (0-25 $m^2$) but rather occurred in the 75-100 $m^2$ class. In addition, our gap size distributions were negatively skewed, particularly within high productivity stands. The distribution of gap sizes within our stands may be due to the average number of gap makers per gap (10-12). This value is higher than the average of 1-5 reported by Pham et al. (2004) but compares to that reported by Kneeshaw and Bergeron (1998). While the number of gap makers per gap reported by these studies were primarily a result of spruce budworm outbreaks, our results are simply a reflection of stand age. Trees are dying due to senescence and gaps are not filling in as quickly due to a slow growing season, resulting in a near normal distribution of gap sizes. Spaces between trees are also larger than in more southern boreal stands (Caron et

al. 2009). In addition, the frequency and distribution of different decay classes between stand types suggests that gap formation is continuous, due to a sequence of small mortality events (Pham et al. 2004, Caron et al. 2009).

Similar to Pham et al. (2004), gaps were generally small (more than 80% of gaps were less than 200 $m^2$). In high productivity stands, trees tend to have more rapid height growth than in low productivity stands (Robichaud and Methven 1993), which may lead to earlier stand break-up. Greater growth in these stands leads to trees reaching greater heights, making them more susceptible to windthrow (Ruel 2000, Boucher et al. 2006,) than in the less productive stands. These larger trees, as well as the higher rates of mortality, could thus be expected to cause larger gaps. This is also evident when looking at gap-maker volume, in which high productivity stands had four times the volume of coarse woody debris than stands of lower productivity.

In contrast with de Romer et al. (2007), we found no correlation between regeneration density and gap size. Since balsam fir is susceptible to moisture-stress when growing in open or dry areas (Frank 1990, McLaren and Janke 1996) it is not surprising that its density did not increase with gap size. Also, boreal forests at these northern latitudes largely have open canopies, thus light is not a limiting factor for regeneration. Differences in light reaching the forest floor between gap and non-gap areas have been found to be small (Harper et al. 2003, St.Denis 2008).

### 1.4.2 Species Response

Much of the literature on gap dynamics in the boreal forest examines the influence of specific stand factors (e.g. light) and/or disturbance (e.g. wind and spruce budworm) on species response. However these factors are less important in areas such as Labrador where light is not limiting due to the relatively open canopy. Nonetheless, we expected gap size and productivity to be the major factors determining species replacement in these stands. However, when gap size and stand productivity were tested, productivity was the principal factor affecting the replacement patterns. While there was no difference in total conifer density, species densities changed significantly between stands of different productivity. These differences may be indicative of the different soil and topographic features in each stand, which create diverse vegetation assemblages. Black spruce was more abundant in low and medium productivity stands, likely since it can grow under a wider range of environmental conditions than balsam fir (Viereck and Johnston 1990). Wilton (1965), Damman (1967) and Foster (1984) found eastern boreal forest plant communities were mainly determined by moisture and drainage. Simon (2005) found balsam fir was mainly present in stands with higher elevations, steeper slopes and high timber volume – corresponding to our high productivity stands.

Runkle (1981) stated reciprocal replacement would likely occur in species-poor stands and Pham et al. (2004) found this was sometimes the case in the northeastern boreal forest of Quebec. However reciprocal replacement does not appear to occur in the northern boreal forests of Labrador. Instead the proportion of gap-fillers mirrors the proportion of gap-makers, indicating cyclical and self-replacement and no shift in species composition. Further,

the broad range and distribution of decay classes indicates a continuous pattern of tree death, and thus gap creation. This is thus, similar to Harper et al. (2003) who found that species replacement patterns are largely structural, rather than compositional.

## *1.5 Conclusion*

Gaps within high latitude boreal forests, particularly in Labrador, are relatively small, but frequent. This can be attributed to: 1) Shorter growing seasons, therefore slower regeneration and filling in of gaps; 2) open canopies due to larger interstitial spaces between trees; and 3) the narrow conical crown of these species (black spruce and balsam fir). It is not surprising then that gaps do not influence patterns of species replacement within these stands, but that productivity does. These results indicate that gap characteristics are not a useful indicator of forest succession in these high latitude boreal forests. Further, productivity is the main factor determining species replacement patterns in these forests. Forest management systems that aim at emulating natural gap-phase dynamics may not influence regeneration patterns in these forests. However since gap formation creates structural heterogeneity, an important factor for wildlife habitat (Kuuluvainen 2002), traditional even-aged forest management (i.e. clearcutting) may need to be adapted to maintain this forest structure.

# GENERAL CONCLUSION

Research has found that gap dynamics play an important role in boreal forests, particularly in areas that have escaped large-scale disturbance for long periods of time (McCarthy 2001, Pham et al. 2004). Much of this earlier research examines the influence of specific abiotic factors (e.g. light) and/or disturbance type (e.g. wind and spruce budworm) on species response. While the range of observed gap patterns (e.g. size and frequency) is often similar between areas, the resulting regeneration patterns are not always equivalent. The patterns created by gaps can also be significantly affected by stand conditions, which in turn affects species composition, tree size, and their susceptibility to wind and pathogens. Thus in Labrador, where the fire cycle is long and insect epidemics are rare, it was reasonable to predict that both gap size and stand productivity would influence species replacement patterns. Our results, however, indicate that productivity was the principal factor affecting the replacement patterns, while gap size had little, if no affect on conifer seedling density. This is not surprising as it has been shown that above ground light levels are higher beyond gap edges in high latitude forests (Ban et al. 1998). Further, in other boreal forests, light levels did not vary with gap size (St Denis 2008). While light has been shown to be one of the major factors driving compositional dynamics in other forests, the lack of light differences in boreal gaps and the fact that both fir and spruce are shade tolerant suggests that gap size does not influence forest dynamics in this region. Alternatively, stand differences lead to different growth rates, and since black spruce and balsam fir have different nutritional needs (Burns and Honkala 1990) their replacement within these stands depends on stand productivity. This finding is in contrast to Pham et al. (2004) who found that

species composition prior to gap formation led to alternate species replacement instead of the self-replacement that we observed.

Gap sizes were generally small and gap fraction was large (47%) yet comparable to other areas (Harper et al. 2006, St. Denis 2008). However the gap size distribution did not follow the common, negatively skewed distribution curve. Rather the distribution of our gap sizes was near normal, owing to slow tree death due to senescence and gaps not filling in as quickly due to a short growing season.

The proportion of gap-fillers to gap-makers indicates cyclical replacement, rather than reciprocal replacement, in the northern boreal forests of Labrador. The proportion of gap-fillers mirrors the proportion of gap-makers, indicating cyclical and self-replacement and no shift in species composition. The broad range and distribution of decay classes also indicates a continuous pattern of tree death, and thus gap creation. This is thus, similar to Harper et al. (2003) who found that species replacement patterns are largely structural, rather than compositional.

Further investigation of tree-ring patterns indicates that regeneration establishment is quite regular in time since 1940, with the absence of common periods of regeneration recruitment. This implies a continuous tree replacement process for both balsam fir and black spruce. These patterns differ from those following spruce budworm outbreaks, where tree recruitment occurs in peaks closely linked with the outbreak events. Thus, the natural disturbances triggering tree replacement in our stands occur at regular intervals on a small scale, such as tree senescence. Tree replacement is thus more similar to temperate and tropical forests, where

mortality and recruitment is due to senescence and is constant through time, than with other boreal forests experiencing exogenous disturbances such as spruce budworm outbreaks.

**Implications for Forest Management**

Forest management systems that aim at emulating natural gap-phase dynamics may not mimic natural regeneration patterns in these forests. Since gap formation creates structural heterogeneity, an important factor for wildlife habitat (Kuuluvainen 2002), traditional even-aged forest management (i.e. clearcutting) may need to be adapted to maintain forest structure. It may be possible to emulate gaps using partial harvesting by creating artificial openings that represent a natural distribution of gap sizes (Coates and Burton 1997). For example, harvested areas could range between 60 and 140 $m^2$, depending on the productivity of the stand being harvested. However, the complex structural heterogeneity, in the form of snags, coarse woody debris, and advance regeneration, play a significant role in the maintenance of gap-phase dynamics (Kuuluuvainen 2002) and may be difficult to emulate during forest harvesting. Though the highest wood loss (in coarse woody debris) is in the high productivity stands, these stands favour the growth of balsam fir, a tree that is of lower commercial value. This, plus the slow growth of these forests, and high wood costs in this region, could suggest that such a strategy may not be economically viable. However, further studies within these forests would provide added evidence to support this .

# Appendix A

## Additional Figures

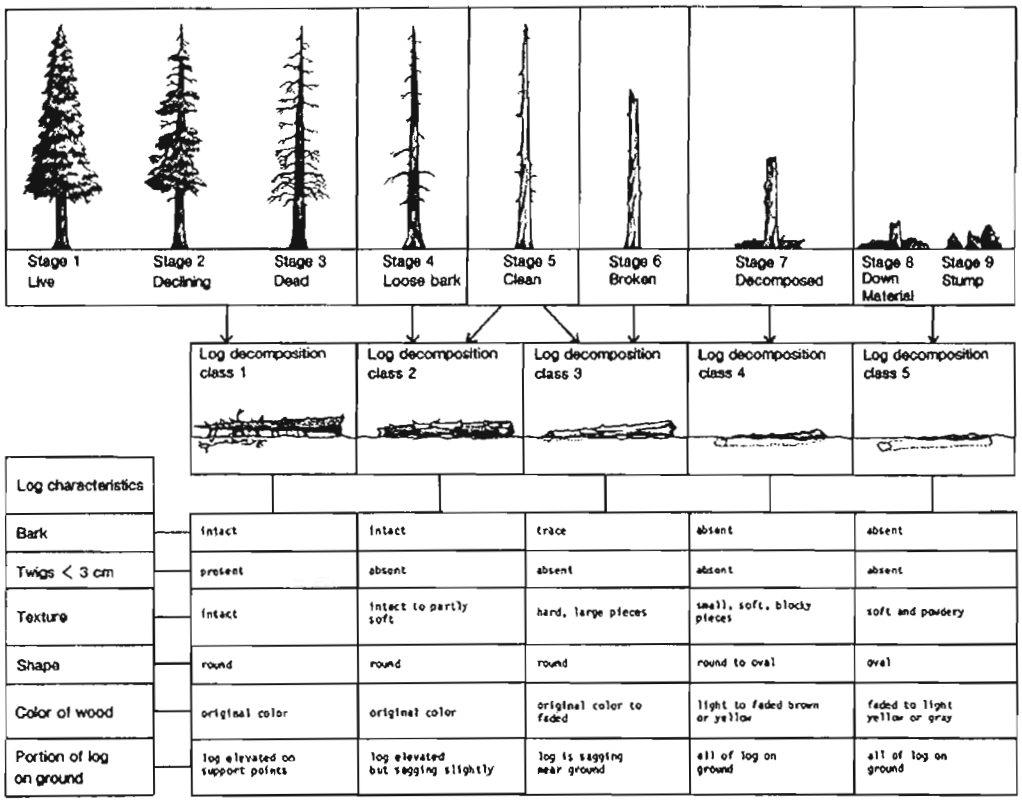



**Figure A1** – Decomposition classes (from Hunter 1990).

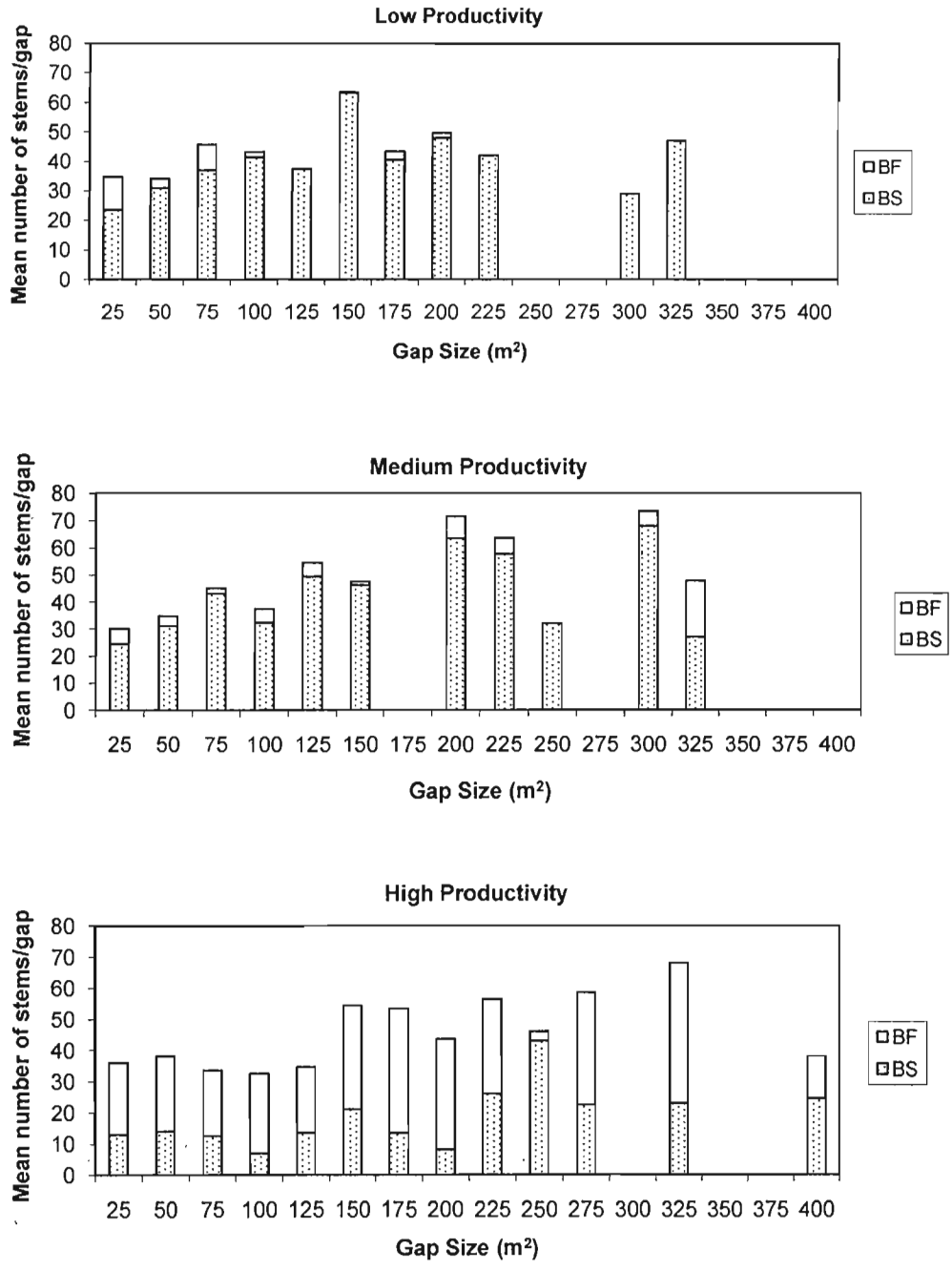



**Figure A2** – Average number of gap-fillers per gap size class ($m^2$) for low, medium, and high productivity stands. BF = Balsam fir and BS = Black spruce.

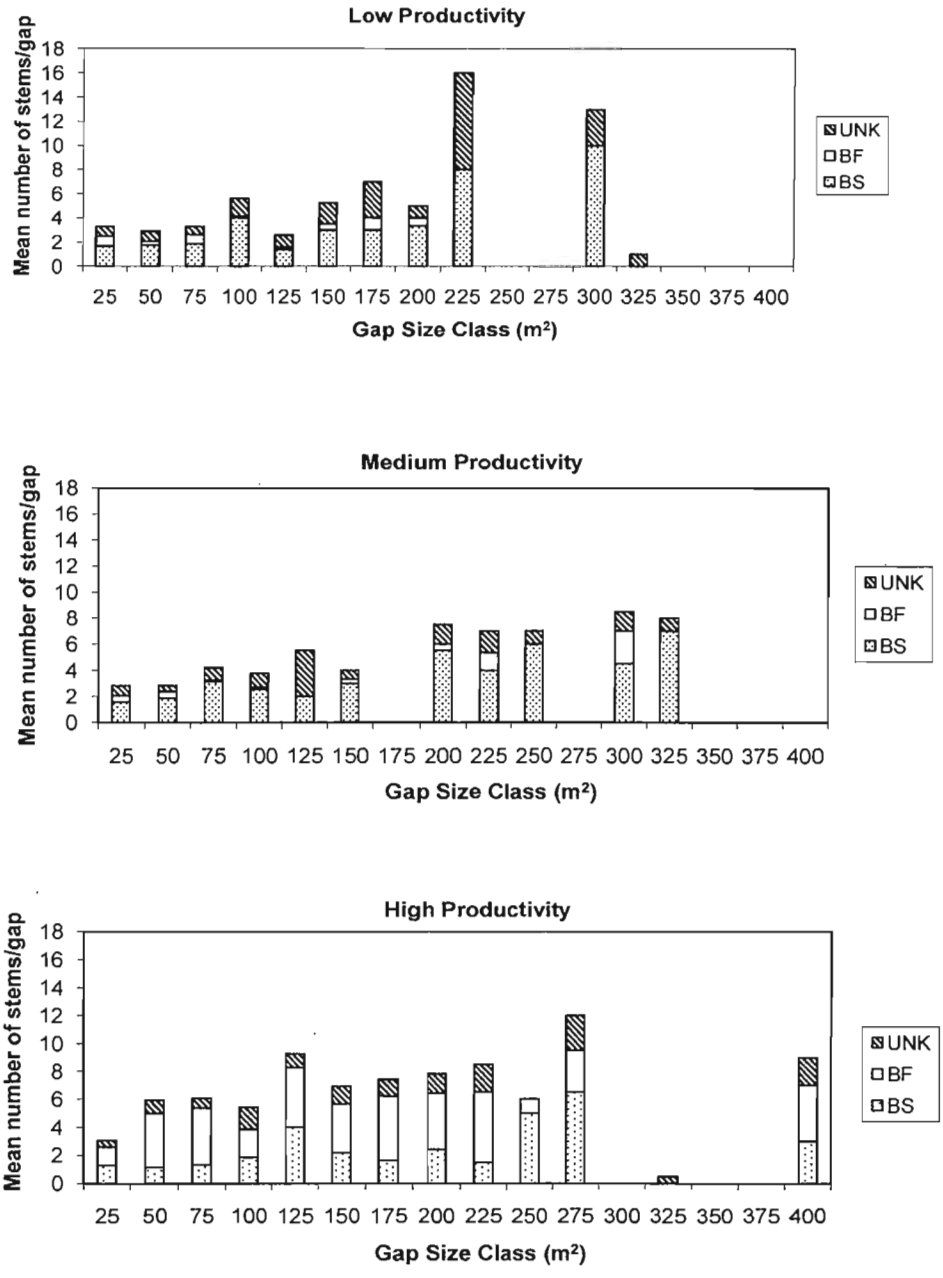



**Figure A3** – Average number of gap-makers per gap size class ($m^2$) for low, medium, and high productivity stands. UNK = unknown, BF = Balsam Fir, BS = Black Spruce

# Appendix B

## Dendrochronological Evaluation of Gap Formation through Time

## Objectives

An intensive examination of the tree rings of regenerating black spruce and balsam fir within a subset of gaps will allow for a better understanding of the temporal replacement patterns within these stands. The purpose of the following section is to determine whether the establishment of regeneration within gaps in these stands was due to a single exogenous event that was synchronous between gaps (e.g. a wind storm or insect outbreak), or due to multiple and discrete events (i.e. senescence).

## Methods

Canopy gaps were grouped into 1 of 7 classes based on gap size: 1 = 0 - 50, 2 = 50 - 100, 3 = 100 - 150, 4 = 150 - 200, 5 = 200 - 250, 6 = 250 - 300 and 7 > 300 $m^2$). To sample a range of gap sizes in each stand type, specific gaps were chosen using the midpoints of the first 4 classes (2 each in class 1 and 2, 3 and 1 in class 4), representing > 90% of the total gap sizes (N=21). Gaps greater than 200 $m^2$ were excluded since they are infrequent within these stands.

Regeneration was measured in alternating variable width belt transects (range 0.5-2 m) perpendicular to the longest axis to obtain 60-100 samples per gap. The belt transect widths were inversely proportional to the number of seedlings present both to ensure an adequate sample size and efficient sampling time. The midpoints of each transect was separated by 2 m along the longest axis.

The species, height, and dbh (for trees > 1.3 m height) of regenerating conifers were measured. Core or disk samples were taken at 0.5 m from the base for trees > 1.3 m tall. To establish a masterchronology and potentially

determine dates of gap maker mortality, approximately 5 - 10 live trees per gap (30 - 40 per stand type) were cored.

The species, length/height, decay class, and mode of mortality (uprooted, snapped while alive, snapped while dead, or standing dead) were recorded for all dead trees (CWD and snags) within each gap. To determine age at death, core or disk samples were taken at 0.5 m in height; however this was impossible for more than half the CWD since decay was too advanced.

Moss depth inside each gap was also compared with that under the canopy to determine potential effects on seedling density. The species and depth of moss to the organic layer was measured at the center point of each belt transect and at four points (north, south, east and west) approximately 10 m outside of each gap.

**Data Analysis**

Using a one-way ANOVA we tested the effect of both species and stand productivity on age of regenerating black spruce and balsam fir stems. A comparison of stems aged using both bud scar count and dendrochronology revealed that stems equal and less than 50 cm in height had equivalent age readings using either technique. Thus, the data of those stems aged by bud scars, equal to or smaller than 50 cm in height, were grouped with the dendrochronological ages and compared among stand type and species.

Average growth rates were calculated and compared with gap size using linear regression. Average growth rates were also compared with stand productivity and conifer species using an interaction plot and tested using a General Linear Model with average growth rate as the response variable.

We used the standard percent-increase method to find evidence of release for regenerating black spruce and balsam fir:

$$\text{Percent increase} = \frac{\text{Mean}_{t2} - \text{Mean}_{t1}}{\text{Mean}_{t1}} \times 100$$

Where $\text{Mean}_{t1}$ is the mean radial growth during the time window prior to the release and $\text{Mean}_{t2}$ is the mean radial growth following the release. A minimum of 5 years was used for time windows of release/suppression. Most regenerating trees were only 10-20 years of age.

## Results

There was a significant difference between the ages of regenerating black spruce and balsam fir ($P = 0.006$), as well as between total regeneration age and stand productivity ($P = 0.001$). The mean ages of both black spruce and balsam fir were higher in low and medium productivity stands than in high productivity stands (Table B1).

**Table B1** – General statistics of the age of regenerating black spruce and balsam fir

| Species | Stand Productivity | N | Mean Age | Standard Error | Minimum Age | Maximum Age |
|---|---|---|---|---|---|---|
| Black Spruce | low | 502 | 18.31 | 0.70 | 1 | 114 |
| | medium | 306 | 19.34 | 0.92 | 2 | 102 |
| | High | 124 | 13.40 | 1.22 | 2 | 83 |
| Balsam Fir | low | 58 | 24.22 | 4.45 | 2 | 135 |
| | medium | 58 | 21.16 | 3.97 | 2 | 151 |
| | High | 266 | 17.27 | 1.44 | 1 | 159 |

There was a significant difference in the average growth rate of regenerating stems between both stand productivity ($P = 0.00$, $R^2 = 0.17$, $F = 21.54$) and species ($P = 0.00$, $R^2 = 0.11$, $F = 26.17$). The growth rate of balsam fir was higher than that of black spruce in both low and high productivity stands, while the growth rates of both were equivalent in medium productivity stands (figure B1). A test for equal variance indicated a significant difference between stand types ($P = 0.00$) which may explain the growth rate results for medium productivity stands (figure B2).

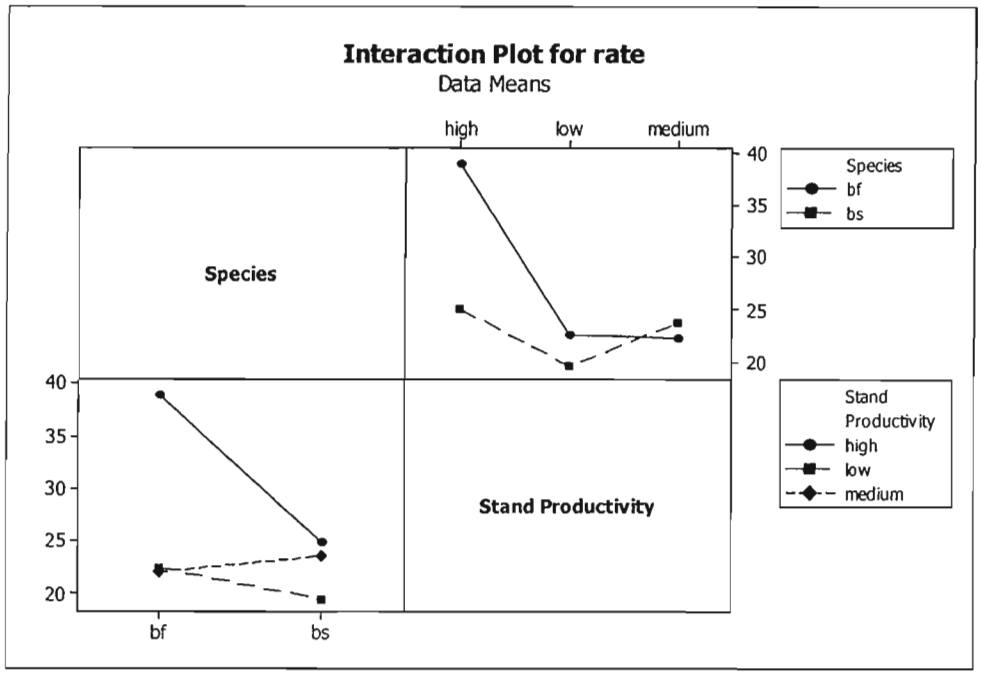



**Figure B1** – Interaction plot comparing average growth rate with stand productivity and species.

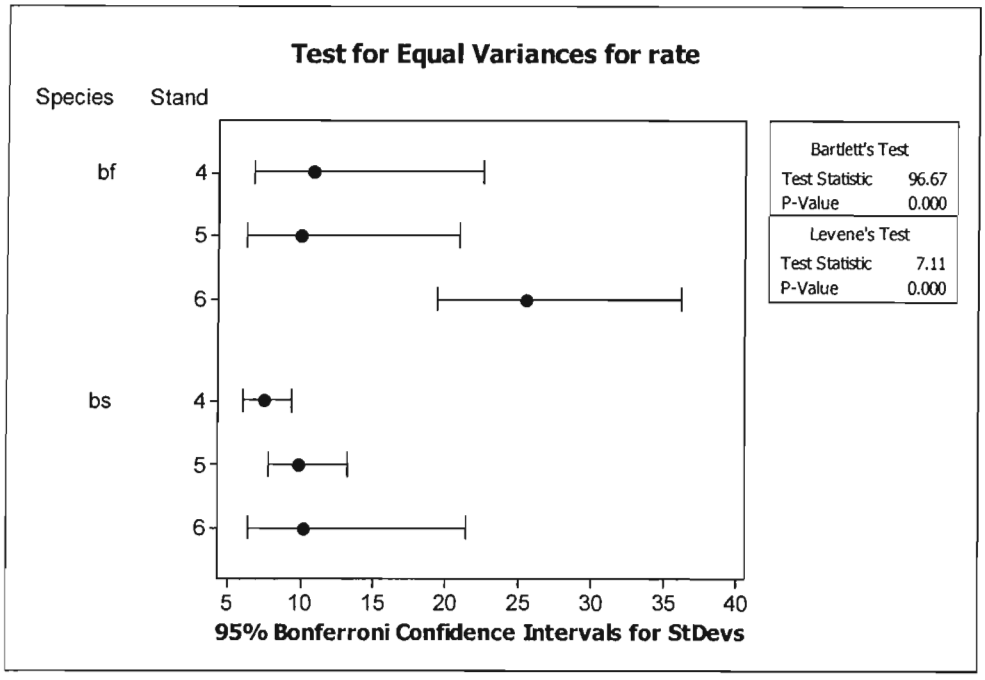



**Figure B2** – Test for equal variances for both balsam fir (bf) and black spruce (bs).

Few of the sampled regenerating trees showed evidence of release between the years 1880 – 1990 (Figure B3). Approximately 50% of the regenerating trees demonstrated release between 1990 – 2000, and this occurred in all three productivity stands. This appears to be due to a single event causing the release of regenerating black spruce and balsam fir. However, this event cannot be determined based on the causes of mortality identified for the gap-makers in this study. Further, this peak may partly be a result of a larger sample size collected during this period.

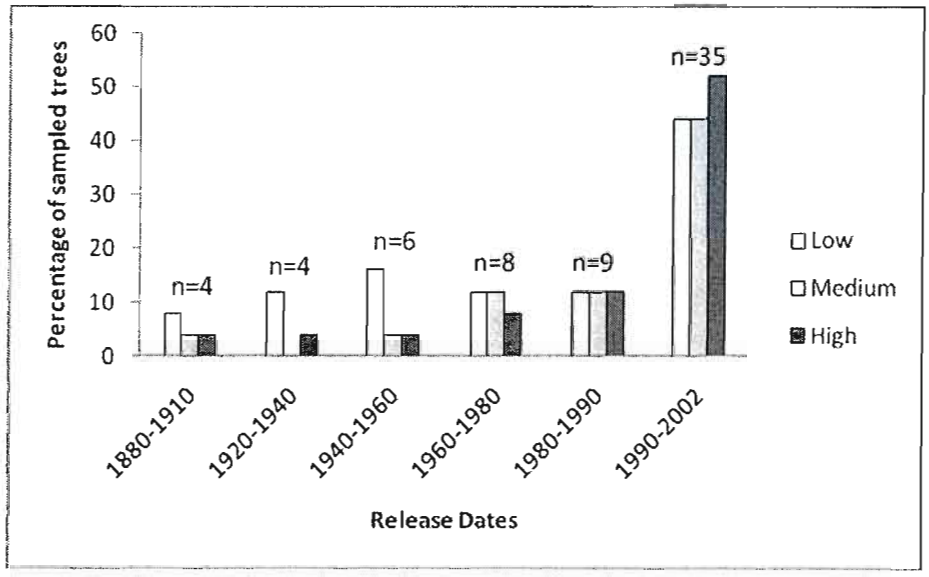



**Figure B3** – Percentage of sampled trees showing evidence of release

Regenerating black spruce and balsam fir had a positively skewed age distribution, with an average age of 18 and only 6 % of stems were older than 50 years of age (figure B4). When these stems were grouped into age classes and compared among stand productivity type, all three stands had a similar distribution of age classes (figure B5). However low productivity stands had a higher number of stems 0-25 years of age, medium productivity stands had a higher number of stems 50-75 years of age, while high productivity stands had a higher number of stems over 100 years of age.

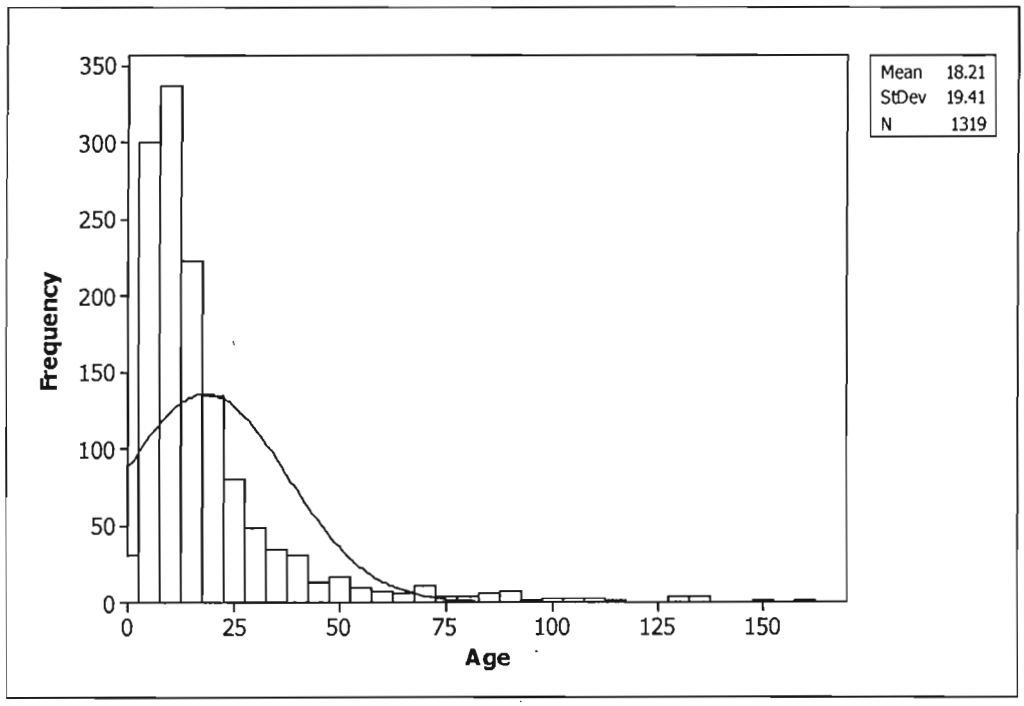



**Figure B4** – Age distribution of total conifer regeneration for all three productivity stands.

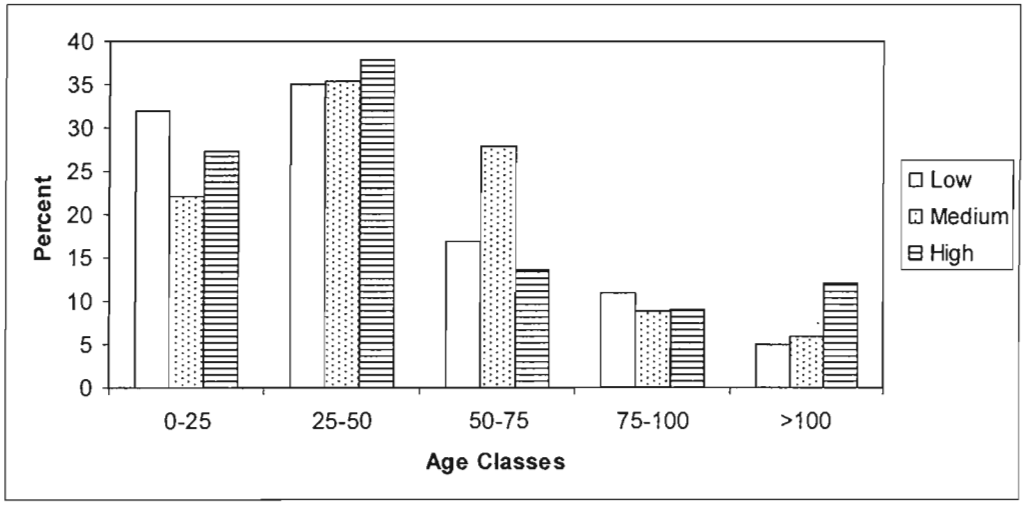



**Figure B5** – Percentage of black spruce and balsam fir regeneration by age class for low, medium, and high productivity stands.

There was no significant difference in average moss depth from inside to outside each gap for all three productivity types ($P = 0.323$, $R^2 = 0.024$, $F = 1$) (Table B2). The major species of moss within each gap included: *Pleurozium schreberi*, *Ptilium crista-castrensis*, *Hylocomium splendens*, *Dicranum* spp., *Sphagnum* spp., and *Cladonia* spp.

**Table B2** – Average moss depth (cm) both inside and outside each gap for low, medium, and high productivity stands.

| Productivity | Transect | Gap | Inside gap (cm) | Outside Gap (cm) |
|---|---|---|---|---|
| Low | 1 | 16 | 13.63 | 9.50 |
| Low | 2 | 1 | 6.96 | 9.25 |
| Low | 3 | 7 | 9.71 | 12.25 |
| Low | 4 | 9 | 8.80 | 8.50 |
| Low | 4 | 16 | 11.00 | 15.63 |
| Low | 5 | 10 | 10.50 | 12.75 |
| Low | 6 | 9 | 4.86 | 6.25 |
| Medium | 1 | 5 | 11.14 | 9.25 |
| Medium | 2 | 5 | 10.38 | 12.00 |
| Medium | 4 | 1 | 10.42 | 15.25 |
| Medium | 5 | 6 | 11.25 | 11.75 |
| Medium | 6 | 8 | 6.34 | 5.88 |
| Medium | 6 | 18 | 7.79 | 7.00 |
| Medium | 7 | 3 | 14.00 | 13.50 |
| High | 1 | 7 | 7.89 | 8.25 |
| High | 2 | 13 | 8.00 | 8.25 |
| High | 3 | 8 | 9.40 | 7.00 |
| High | 4 | 11 | 12.29 | 14.25 |
| High | 5 | 4 | 17.40 | 16.25 |
| High | 5 | 15 | 13.17 | 18.75 |
| High | 6 | 18 | 9.40 | 14.25 |

## Preliminary Discussion

In low and medium productivity stands, where black spruce dominates the canopy, self-replacement is occurring. In high productivity stands balsam fir appears to be replacing black spruce. However, this may not indicate reciprocal replacement, but rather structural change, since there was a large presence of balsam fir already in the canopy (Harper et al. 2003, Kneeshaw and Gauthier 2003). These old-growth stands containing a mixture of size and age classes are considered to be in a state of equilibrium, where growth is balanced by mortality (Wilton 1965).

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